

GENETICS OF MARQUIS $\times$ TURKEY WHEAT
IN RESPECT TO BUNT RESISTANCE, WINTER HABIT
AND AWNLESSNESS

BY

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GENETICS OF MARQUIS $\times$ TURKEY WHEAT IN RESPECT TO BUNT RESISTANCE, WINTER HABIT, AND AWNLESSNESS¹

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INTRODUCTION

It is generally understood that varieties of wheat vary in their ability to resist attacks of bunt, *Tilletia tritici*, (Bjerk.) Wint. Three distinct types of resistance have been observed at the Washington Agricultural Experiment Station. The first type is that of the resistant winter wheat which, when spring sown, is immune; the second is that of the wheat which possesses the same relative resistance or susceptibility, whether fall or spring sown; the third and most remarkable type is that of the resistant spring wheat which, when fall sown, is quite susceptible.

INHERITANCE OF BUNT RESISTANCE

In order to clearly show the three types of resistance, Table I has been compiled from the records of experimental work on comparative resistance of American wheats, conducted at Pullman, Wash., in cooperation with the Office of Cereal Investigations, Bureau of Plant Industry, of the United States Department of Agriculture. Part of this material has been published in United States Department of Agriculture Bulletin 1299 (15).²

TABLE I.—*Comparative bunt resistance of fall and spring sowings of several wheat varieties*

Name of variety	Washington No	Year	Percent of bunt		Type
			Fall	Spring	
Marquis.....	576	1919	74	10	3
Do.....	576	1921	77	7	3
Florence.....	634	1919	8	8	2
Bluestem.....	362	1919	90	92	2
Dicklow.....	630	1919	95	96	2
Early Baart.....	618	1919	76	87	2
Little Club.....	500	1919	96	97	2
Jenkin.....	526	1919	89	94	2
Red Chaff.....	421	1919	97	94	2
Hybrid 128.....	592	1921	94	(a)	-----
Winter Fife.....	371	1921	94	(a)	-----
Hybrid 143.....	590	1921	97	(a)	-----
Turkey.....	326	1921	10	0	1

* Did not head.

¹ Received for publication July 2, 1925; issued February, 1926. Revised from junior writer's thesis submitted for degree of master of science. The work has been done under the direction of the senior writer. The compilation of data and review of literature were done largely by the junior writer. Published with the approval of the director of the Washington Agricultural Experiment Station as Scientific Paper No. 121, College of Agriculture and Experiment Station.

² Reference is made by number (italic) to "Literature cited," p. 181.

Turkey represents the first type, which is resistant when fall sown but immune when spring sown. This variety is awned, and has the winter habit of development, i. e., if sown the latter part of April it will not head the following summer but remains a green grass clump, while Marquis heads and matures seed about the first of August.

With the exception of Marquis, all other varieties which matured from both fall and spring sowings represent the second type and possess practically the same relative amount of resistance regardless of time of sowing. Marquis alone represents the third type, which is resistant when spring sown but quite susceptible when fall sown. This variety is awnless and has the spring habit of growth. However, its susceptibility is not complete as is shown by the fact that it produced only 77 per cent of bunt the same season in which the three varieties, Hybrid 128, Winter Fife, and Hybrid 143, produced an average of 95 per cent. These three varieties have been considered as having practically no resistance (6). The difference, then, of 18 per cent in favor of Marquis may be taken as an indication that it is not completely susceptible but does possess some resistance. Similar evidence has been reported (8) in a cross between Hybrid 128 and Marquis. Of nine F_3 families comparatively low in amount of bunt produced, five produced the smallest percentage of bunt of the 13 rows in the F_4 generation. Of four very smutty F_3 families selected, one produced the highest percentage of bunt in the F_4 generation, and two produced more than the average of all F_4 rows in 1920. Five plants selected from the least smutty and five from the most smutty F_4 row produced an average of 78 and 91 per cent of bunt, respectively, in the F_5 generation in 1921. Since Hybrid 128 has no resistance, it seems that the difference was caused by a factor for resistance possessed by Marquis that is not affected by the winter resting period.

From previous studies (7, 8) it seems that bunt resistance in some wheat varieties is not a simple Mendelian unit character, but that if Mendelian it is composed of multiple factors because a continuous series ranging from complete immunity to complete susceptibility was obtained. Apparently different wheats possess different kinds of resistance. Transgressive inheritance occurred in a cross between Turkey and Florence. From these two resistant wheats, segregates varying from immunity to 86 per cent bunt were obtained in the F_3 generation. Some of the immune segregates have bred true for immunity through nine generations (9).

Unlike many other parasitic fungi, bunt is not known to exist in more than one biologic form. Unless other forms are discovered, the problem of breeding for bunt resistance is much simpler than breeding for resistance to diseases which consist of several biologic forms, like the rusts, for example (10, 11, 12, 14).

INHERITANCE OF WINTER HABIT

Cooper (4) reports finding the short vegetative period to be dominant over the long one in crosses between spring and winter wheats. Marquis, when crossed with three different winter wheats, produced approximately 13 spring plants to three winter in the F_2 generation. He explained this segregation on a two-factor basis in which one factor is dominant for winter and the other is an inhibitor of the

winter habit. The F_2 generation was satisfactorily analyzed on the foregoing assumption, but all three classes expected were not obtained in the F_3 generation, and two of the 13 F_3 families did not segregate according to any of the expected ratios. The small number of plants in the F_2 and the small number of families in the F_3 , part of which were not explainable on his assumption, make it seem probable that other factors had a modifying influence.

In a cross between Marquis and Kanred, Aamodt (1) was unable to analyze the segregation on a definite factorial basis. However, he does conclude that the segregation for growth habit accords with Mendelian laws and that the results indicate multiple factors. The investigations of Vavilov and Kouznetsov (16) are similar to those of Aamodt. In the F_3 generation they found 9,551 spring plants to 2,191 winter plants, indicating the dominance of the spring form.

INHERITANCE OF AWNLESSNESS

In order to study the reaction of the Turkey parent in crosses with varieties other than Marquis, Table II was compiled from unpublished data obtained by the writers in other experiments.

TABLE II.—Segregation of awnless and awned plants in the F_2 generation of crosses between Turkey and six other varieties of wheat

Name of cross	Year	Number of plants awnless	Number of plants awned	Per cent awned
Fortyfold $\times$ Turkey.....	1919	423	175	29.3
Turkey $\times$ Triplet.....	1920	1,218	435	26.3
Triplet $\times$ Turkey.....	1920	1,101	380	25.7
Turkey $\times$ Ruddy.....	1920	999	306	23.4
Ruddy $\times$ Turkey.....	1920	1,163	405	25.8
Hybrid 128 $\times$ Turkey.....	1920	1,343	473	26.0
Turkey $\times$ Winter Fife.....	1921	443	154	25.8
Winter Fife $\times$ Turkey.....	1921	423	133	23.9
Turkey $\times$ Jenkin.....	1921	1,155	370	24.3
Total.....	-----	8,268	2,831	25.5

In all crosses of Turkey with the awnless varieties in Table II, the segregation approaches very closely a 3 : 1 ratio of awnless to awned plants. This is especially true when taking the totals of all crosses into consideration. A similar segregation in six other crosses has also been reported by the senior writer (5). The ratio of 3 : 1 proved to be 1 true awnless : 2 intermediate awnless : 1 true awned, by the behavior in the F_3 generation. Percival (13) has also found segregation in numerous crosses of beardless with bearded wheats to approach the 1 : 2 : 1 ratio. If the intermediate variants were classed with the awnless, the 3 : 1 ratio would be obtained. He further reports work of the Howards in which they obtained a segregation of 15 awned or partially awned to 1 quite awnless in a cross between an awned wheat and one which was quite awnless. They interpreted such a segregation as a dihybrid in which there was one factor for short awns and another for elongation for these short awns. However, in a cross in which Marquis is the awnless parent, the quite awnless types would not be expected, because Marquis has short awns from 0.3 to 1 cm. in length upon the upper fourth of the head.

In order to study the possibility of linkage between awns and bunt resistance, Table III was compiled from crosses of Turkey with five wheats other than Marquis which the writers had analyzed during the years 1918 to 1922.

TABLE III.—Percentage of bunt produced by the awnless, mixed, and awned families in the F_3 generation of six crosses

Name of cross	Year	Percentage of bunt		
		Awnless	Mixed	Awned
Turkey×Florence.....	1918	9.9	12.7	14.5
Hybrid 128×Turkey.....	1918	55.1	50.6	43.5
Fortyfold×Turkey.....	1920	46.1	45.3	51.0
Triplet×Turkey.....	1921	55.0	56.8	57.6
Turkey×Jenkin.....	1922	63.6	65.2	(*)
Turkey×Triplet.....	1922	57.9	59.4	(*)

* Only seed from awnless plants sown.

† Only seed from awnless glabrous plants sown.

With the exception of Hybrid 128 × Turkey, it appears that there is some relationship between the presence of awns and increased susceptibility. However, in the exception, it is possible that the extra factor causing the extreme susceptibility of Hybrid 128 is linked with awnlessness, and in this case the awnless families of the F_3 generation would have a tendency to produce more bunt than the intermediate ones and these in turn would produce more than the awned. The apparent association of awns and susceptibility in the five other crosses may be due to one or the other of two things. It is possible that the presence of awns makes it easier to detect bunted plants, and that in the field separations part of the awnless bunted plants were counted as nonmutated. The other is that the awned character of Turkey is actually linked with some susceptibility which is held in check by the chemotactic nature of Turkey resistance, and when the factors for resistance are eliminated in the recombination of chromosomes, the awned plants are more liable to become infected than the others. Regardless of the manner in which this variation was caused, the data indicate that if there is any linkage between the presence or absence of awns and relative amount of resistance, it is too small to interfere materially in selecting resistant plants of any type desired.

Aamodt (1) studied the possibility of linkage between awns and growth habit in his cross between Kanred and Marquis, but found no indication of it.

EXPERIMENTAL DATA

METHODS

The cross between Marquis and Turkey was made in 1918. The F_1 seed was planted that fall, and eight F_1 plants were harvested in 1919. The seed from five of these was sown in separate rows in the fall of 1919, and the F_2 families were harvested in 1920, one of which was selected as the progenitor of the F_3 generation. Approximately 150 seeds from each F_2 plant were infected by rolling the kernels in bunt until no more spores would adhere to them; then each packet was divided into two parts. One part (75 seeds from each plant) was sown in the fall, and the rest in the spring. Four replications of

each parent variety, and three of the F_2 sibs, were grown under the same conditions for comparison.

The F_2 generation was separated into awnless and awned plants, and notes were taken on the F_3 families as to whether the plants in each were all awnless, mixed, or all awned.

To obtain the amount of bunt produced by each row, the method described in 1920 (7) was used, which represents the approximate loss, and is comparable to the percentage obtained by a head count.

When fall sown, Marquis and Turkey head out and ripen at approximately the same date; but when spring sown Turkey does not even head unless sown very early. The fall-seeded F_3 rows headed and ripened uniformly, and all rows were pulled and records taken at one time. However, there was a distinct segregation in the ripening of the spring-sown material, and all plants were pulled and records taken as they ripened. The average date ripe was

computed according to the formula $x = \frac{(bf)_1 + (bf)_2 + (bf)_3 \dots}{N}$ in

which x is the average date ripe, b is the date any given number of plants become ripe, f is the number of plants ripening on a given date, N is the sum of f_1, f_2, f_3 , etc., which make up the total number of plants in the row.

In figuring the coefficient of correlation between any two sets of variants, the general rule of Babcock and Clausen (2) was modified by using class numbers as class centers. Class 1 was used as the assumed mean, and all corrections were made accordingly. Probable

error was figured according to the formula $E = \frac{0.6745 (1 - r^2)}{N}$.

DESCRIPTION OF PARENTS AND F_1 GENERATION

Marquis (Wash. 576) is an awnless spring wheat producing hard red kernels. It is of hybrid origin, being a product of the Central Experimental Farm, Ottawa, Canada. The parents of Marquis are Hard Red Calcutta (an early ripening spring wheat, and Red Fife (a wheat which differs from Marquis in being taller and later, with kernels slightly longer and more pointed) (3).

Turkey (Wash. 326) is an awned winter wheat of the Crimean group. This strain was introduced from Kansas in 1906. It is very similar in taxonomic characteristics to other wheats of the Crimean group, but differs from some other strains in its resistance to bunt. Certain Crimean selections are bunt-free, while others produce as much as 75 per cent of bunt.

The F_1 seed of Marquis $\times$ Turkey was sown in the fall. The F_1 plants all ripened uniformly the following summer. They were all intermediate for awnlessness, having short awns on the upper florets. As the seed was not infected, no data on resistance to bunt were obtained.

DESCRIPTION AND ANALYSIS OF THE F_2 AND F_3 GENERATIONS

BUNT RESISTANCE

Four of the 160 families of the F_3 generation of Marquis $\times$ Turkey consisted of fewer than 10 plants in either the fall or spring sowing, and these were not considered. As was previously stated, three F_2 sibs and four rod rows of each parent were grown under the same

conditions as the F_3 generation. The data on bunt resistance of all material in both the fall and spring plantings are summarized in Table IV.

TABLE IV.—Number of parent replications and F_2 and F_3 families of Marquis $\times$ Turkey falling into each class, when differences between class centers increase by an arithmetical progression of 2.5. This progression emphasizes the small differences of the resistant segregates

Variety	When sown	Class center of bunt										Total
		0	0.5	3	8	15.5	25.5	38	53	70.5	90	
Marquis.....	(Fall.....									3	1	4 replications. Do. Do. Do.
	(Spring.....				4							
Turkey.....	(Fall.....				4							
	(Spring.....	4										3 families. Do. Do.
F_2	(Fall.....								1	1	1	
	(Spring.....			1	2							
F_3	(Fall.....			2	11	21	12	8	28	38	36	156 families. Do.
	(Spring.....	44	16	29	35	21	7	3	1			

In breeding for bunt resistance, a given difference between two resistant segregates is much more significant than the same difference between two susceptible ones. For instance, a variety of wheat which produces an average of 1 per cent of bunt is evidently quite different from a variety which produces 10 per cent, but a variety which produces 70 per cent is not so different from one which produces 80 per cent. Therefore, a factor for resistance has a larger value when acting alone than when acting in cooperation with other resistance factors. As immunity is approached by the accumulation of factors, the value of the individual factor approaches 0, but acting alone it appears to have a value of about 20 per cent. In order to allow each factor its true value, whether acting alone or in combination with other similar factors, the use of an arithmetical progression seemed the more logical method to determine the size of the various classes. The F_3 segregates varied from immune to 100 per cent bunted, and were divided arbitrarily into 10 classes. All immune segregates were placed in the first class, this being 0. The rest of the population fell into nine classes, the last of which has a spread of 20 per cent. A progression of 2.5 between class centers placed the center of the second class at 0.5 per cent and the tenth at 90 per cent.

The resistance of the two parents is shown in Table IV. Marquis is fairly susceptible when fall sown, but does show a small amount of resistance in that three of the four replications were in the 70.5 per cent class. Marquis, when spring sown, falls into the 8 per cent class. Turkey, which falls into the 8 per cent class if fall sown, is immune in the spring sowing.

The F_2 generation was somewhat more resistant than Marquis in both sowings, but was not nearly so resistant as Turkey. However, in the F_3 generation, transgressive inheritance occurred and the spread in both the fall and spring sowings exceeded the extremes of both the parents. The resistance of Turkey does not account for those segregates falling into the 3 per cent class in the fall sowing, and there are too many immune segregates in the spring sowing for Turkey to be the sole contributor. The susceptibility of Marquis does not account for nearly all the segregates in the 90 per cent

class in the fall planting, or for those beyond the 8 per cent class in the spring planting.

The data in Table IV (shown graphically in fig. 1) bring out the similarity of the fall and spring sown F_3 families. In each curve there is a distinct division between the resistant and susceptible segregates. If it were possible to judge the relative resistance of the immune segregates in the spring planting, and the relative susceptibility of all the segregates in the 90 per cent class of the fall planting, each curve could be plotted so that it would drop to the base line at either end of the curve. If such an extension to both curves can be imagined, a striking similarity will be seen between the two. The susceptible part of each curve includes a larger part of the population. The difference in the bunt resistance of parents when fall and spring sown is evidently responsible for the difference in the location of the two curves, which indicates the probability of a similarity in the inheritance of resistance in both sowings.

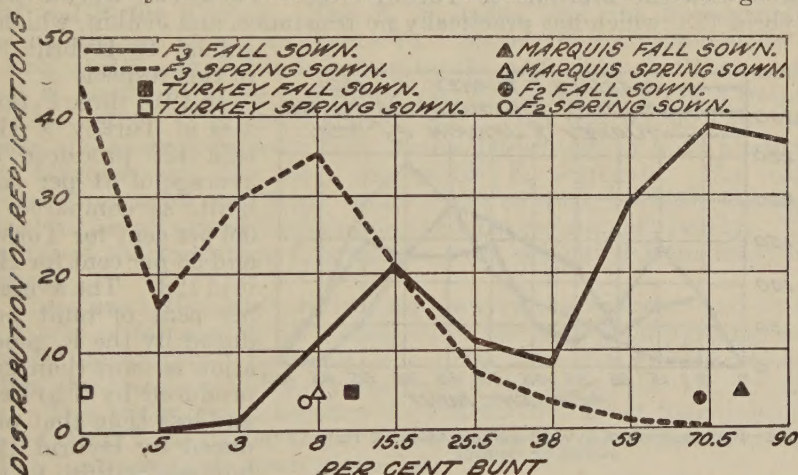


Fig. 1.—Bunt resistance of Marquis, Turkey, and their F_2 and F_3 segregates

In order to determine whether the factors producing resistance in the fall and spring sowings were the same, the coefficient of correlation between the two sowings was worked out as shown in Table V.

TABLE V.—Correlation of 156 F_3 families of Marquis $\times$ Turkey, in respect to bunt resistance in fall and spring sowing

Per cent of bunt in row in fall planting, subject. Per cent of bunt in row in spring planting, relative. Coefficient of correlation, 0.711 ± 0.027

Class centers	0	5	15	25	35	45	55	Fall-sown frequencies
5.	10	2						12
15	19	2	1					22
25	9	2						11
35	1	4						5
45		8						8
55	3	18	1					22
65	1	15	4					20
75		13	7					20
85	1	9	6	4	2			22
95		3	6	3	1		1	14
Spring-sown frequencies	44	76	25	7	3		1	156

The high coefficient of correlation 0.711 ± 0.027 indicates that the varying degrees of resistance in either the fall or spring sowing is influenced by the same factors. The coefficient of correlation for the 88 families which produced no winter plants in the spring sowing was 0.708 ± 0.036 , or practically the same as when all families were considered. The slight difference between the two coefficients is a significant indication of little or no linkage of bunt resistance and winter habit.

FALL-SOWN MATERIAL

From a study of the data already presented, it is evident that the factor for resistance which Marquis possesses plays an important part in the genetics of bunt resistance in this cross. In order to further study the effect of the Marquis factor, two crosses in which an entirely susceptible wheat was crossed with Turkey were compared with the Marquis $\times$ Turkey cross. These two wheats were Hybrid 128, which has practically no resistance, and Jenkin, which is similar to Hybrid 128 in this respect.

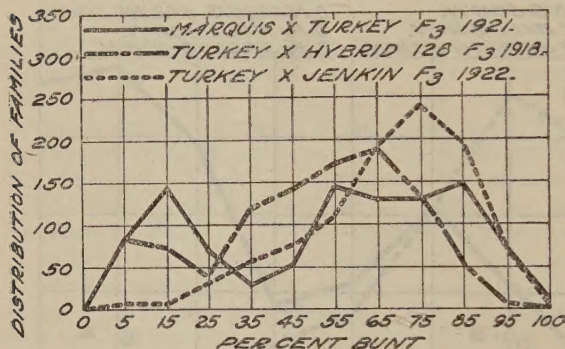


FIG. 2.—Bunt resistance of F_3 families of three crosses of Turkey with susceptible varieties

cent of the susceptible parent. Although 1921 was a much more favorable year for bunt production, the same relationship holds true for the cross between Marquis and Turkey.

The F_3 generation of Turkey $\times$ Hybrid 128 was grown also in 1918, while that of Turkey $\times$ Jenkin was grown in 1922. The distribution of the F_3 segregates in each of the foregoing crosses, together with that of Marquis $\times$ Turkey, are shown in Figure 2. Since the resistant segregates in each of the crosses are few, the distribution is shown by classes in which the class centers vary by 10. This spreads out the susceptible segregates more than if the class centers varied by an arithmetical progression.

There was considerable difference in bunt production of pure lines in 1918 and 1921. In 1918 the average bunt production of Turkey and Hybrid 128 was 0.6 and 63 per cent, respectively (8), while in 1921 it was 10 and 94 per cent (Table I). For this reason the Turkey $\times$ Hybrid 128 cross can not be compared directly with the one between Marquis and Turkey. However, 1921 and 1922 were very similar in that conditions were favorable for bunt production both years, and the F_3 of Turkey $\times$ Jenkin can be compared directly with the

F_3 of Marquis $\times$ Turkey. If the F_3 generation of Turkey $\times$ Hybrid 128 had been grown in 1921 or 1922 the bunt production of all segregates would have been increased, and a curve representing their distribution would be very similar to the one for Turkey $\times$ Jenkin.

The effect of the Marquis resistance working in combination with the Turkey resistance increases the number of resistant families and decreases the number of susceptible ones when compared to a cross in which the susceptible variety possesses no resistance.

Since transgressive inheritance occurred in Marquis $\times$ Turkey, it is evident that the two parents differ in their resistance. The assumption of one factor carried by each parent explains fairly well the distribution of the fall-sown F_3 families.

The resistance of Turkey will be called a , and that of Marquis b , in the discussion which follows. As susceptibility is partially (about three-fourths) dominant, the resistant factors are written as recessive. The genetic composition of the parents is $AAbb$ for Marquis and $aaBB$ for Turkey. The F_1 is $AaBb$, and the F_2 segregates in the manner shown in Table VI. Since the bunt production of $AAbb$, $aaBB$, and $AaBb$, is known by the performance of the parents and F_2 check rows, the remaining genotypes can be given a proportionate value. The value allowed for $AABB$ was 95 per cent, this being the average between the extreme percentage of bunt produced by Marquis and the most susceptible F_3 segregate. The value allowed for $aabb$ was 5 per cent, or the average between the most resistant check row of Turkey and the most resistant F_3 family. The values of the remaining four classes were computed from these five classes.

There are rather wide differences between the expected and actual numbers of families in each class when the nine genotypes are considered separately. However, the differences are greatly reduced when the classes are added according to the genotypes AA , Aa , and aa . This is significant because the a factor has about four times the value of the b (Marquis) factor in inhibiting the development of bunt when the parents are sown in the fall.

TABLE VI.—Genotypes of the F_2 generation of fall-sown Marquis $\times$ Turkey as shown by performance of the F_3 families; also per cent of bunt expected from each genotype if each parent carries a different factor for resistance

Genotype	Per cent bunt expected	Per cent population	Spread of class (per cent)	Number of families	
				Actual	Expected
$AABB$	95 (assumed)	6.25	93 to 100	7	9.75
$AABb$	90 ^a	12.50	84 to 92	24/46	19.50/39
$AAbb$	77 Marquis	6.25	76 to 83	15	9.75
$AaBB$	74 ^b	12.50	72 to 75	6	19.50
$AaBb$	69 (F_2)	25.00	65 to 71	18/61	39.00/78
$Aabb$	59 ^c	12.50	36 to 64	37	19.50
$aaBB$	10 Turkey	6.25	8 to 35	14	9.75
$aaBb$	9 ^d	12.50	8 to 35	29/49	19.50/39
$aabb$	5 (assumed)	6.25	0 to 7	6	9.75

^a $95-77=18$. 75 per cent $\times 18=13$. $77+13=90$.

^b $95-10=85$. 75 per cent $\times 85=64$. $64+10=74$.

^c $77-5=72$. 75 per cent $\times 72=54$. $54+5=59$.

^d $10-5=5$. 75 per cent $\times 5=4$. $4+5=9$.

The value of a factor in heterozygous condition is $\frac{69}{95}$ (or 75 per cent) of one in homozygous condition.

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The seasonal fluctuations of *a* and *b* explain the difficulty of classifying each segregate, and accounts for the differences found. Fluctuations greater than 20 per cent occurred in the Marquis check rows and in the F_2 sibs. It is logical to expect that similar fluctuations might occur in the F_3 segregates.

The foregoing statements bring out some of the difficulties encountered in attempting to interpret the inheritance of bunt resistance on a factorial basis. Seasonal and individual fluctuations of standard varieties are so great that several years' data on a large population would have to be taken into consideration in order to prove such an interpretation satisfactorily. It fits fairly well the small population of the F_3 generation grown in 1921. It also suggests that resistance reacts as a dihybrid in the cross between Marquis and Turkey.

SPRING-SOWN MATERIAL

The date of sowing in the spring was so early that some of the Turkey plants headed and ripened late in the summer. These plants were all immune. The resistance of spring-sown Marquis was high, the bunt production being but 8.5 per cent. The F_2 generation produced 7.2 per cent bunt, while the 156 F_3 families produced an average of 6.7 per cent as compared with 54.4 per cent in the fall-sown division. Since the coefficient of correlation between the fall and spring sown material was so high, each individual family produced considerably less bunt in the spring planting. However, this is to be expected because both parents show the same thing.

Transgressive inheritance was more noticeable in the spring-sown material. Thirty-one of the F_3 families were more susceptible than the most susceptible Marquis check row. One of these produced 55 per cent bunt or five times as much as spring-sown Marquis has ever produced in the writers' tests at Pullman.

It seems probable that the factors influencing the resistance of the spring-planted material are the same as those influencing the fall-sown, since the coefficient of correlation between the bunt production of the two plantings is high. (0.711 ± 0.027 , Table V.)

In both parents resistance appears to be partially dominant in the spring sowing, but in order to prevent confusion, the genetic composition is written the same as for the fall sowing, i. e., Marquis AAbb and Turkey aaBB. The segregation of the F_2 generation as shown by the F_3 performance is given in Table VII. The value of AaBb was assumed to be 40 per cent, which is approximately the average of the two most susceptible classes. As there were only four families in these two classes, it was assumed that they were the same genetically. The value for each of the remaining genotypes was taken or computed from the bunt records of the parents and the F_2 sibs.

TABLE VII.—Genotypes of the F_2 generation of spring-sown Marquis $\times$ Turkey as shown by performance of the F_3 families; also per cent of bunt expected from each genotype if each parent carries a different factor for resistance

Genotype	Per cent bunt expected	Per cent population	Spread of class (per cent)	Number of families	
				Actual	Expected
AABB.....	40 (assumed).....	6.25	32 to 55.....	4	9.75
AABb.....	14 ^a	12.50	12 to 31.....	22	19.50
AAbb.....	8 (Marquis).....	6.25	3 to 11 ^b	9	9.75
AaBB.....	8 ^c	12.50	3 to 11 ^b	18	19.50
AaBb.....	7 (F_2).....	25.00	3 to 11 ^b	36	39.00
Aabb.....	1.6 ^d	12.50	0.1 to 2.....	23	19.50
aaBB.....	0 (Turkey).....	6.25	0.....	11	9.75
aaBb.....	0 ^e	12.50	0.....	22	19.50
aabb.....	0 ^f	6.25	0.....	11	9.75

^a 40-8=32. 20 per cent $\times$ 32=6. 6+8=14.

^b Since one of the F_2 segregates produced only 3 per cent bunt, the F_3 families producing this amount or more are not included in class Aabb.

^c 40-0=40. 20 per cent $\times$ 40=8. 8+0=8.

^d 8-0=8. 20 per cent $\times$ 8=1.6. 1.6+0=1.6.

^e Probably "more immune" than Turkey.

^f Probably "more immune" than aaBb.

The value of each factor in heterozygous condition is $\frac{7}{40}$ (or practically 20 per cent) of the homozygous condition.

On account of the genotypes AAbb, Aabb, and AaBb having approximately the same value, they could not be distinguished and were taken all together. However, each was allowed its proportionate part of the population falling into the general class expected from the three. The genotypes aaBB, aaBb, and aabb, were handled in the same way.

Considering that the expected class centers were close together, and that the fluctuations in bunt production of Marquis and the F_2 sibs were 3 and 7 per cent respectively, it seems that the dihybrid assumption accounts for the distribution of the spring-sown F_3 families even better than it does for these same families when fall sown.

WINTER HABIT

The F_1 and F_2 generations of Marquis $\times$ Turkey were grown from fall sowing. The F_3 families were grown in duplicate, and half of the seed of each F_2 plant was sown in the fall and the other half in the spring. Three F_2 sibs and four check rows of each parent were grown under conditions comparable with both sowings of the F_3 generation.

The spring sowing was done so early (April 1), that some of the Turkey plants headed and ripened. This fact makes a definite separation of the winter and spring plants difficult. If this planting had been two weeks later the Turkey would not have headed and the segregation would have been unmistakable.

The fall-sown material ripened uniformly, and no data were taken regarding any small differences in the date of ripening. However, marked differences were noticed in the spring-sown material, and the ripe plants were pulled and recorded weekly. The first date of ripening was August 2, and the last was August 29. Those plants which were still green or had not headed at this late date were recorded as winter. The numbers of plants of the parents, F_2 sibs, and F_3 generation which were ripe on each date are shown in Table VIII.

TABLE VIII.—Number of plants ripening weekly—of Marquis, Turkey, the F_2 sibs, and the F_3 families

Description	Number of plants ripe each date					Number of winter plants
	Aug. 2	Aug. 9	Aug. 16	Aug. 23	Aug. 29	
Marquis	22	89	89	2	0	0
Turkey	0	0	0	0	24	92
F_2	32	78	117	16	4	4
F_3	262	1,263	3,763	498	365	456

The similarities and differences in time of ripening are shown, on a percentage basis, in Figure 3. There is no overlapping of the parents, and their extremes are obtained in both generations.

The F_2 and F_3 generations are similar in the percentages of plants ripe on each date. The Marquis plants were practically all ripe by August 16, while those of Turkey were all in the August 29 and winter classes. The curve of the F_2 and F_3 generation is not midway

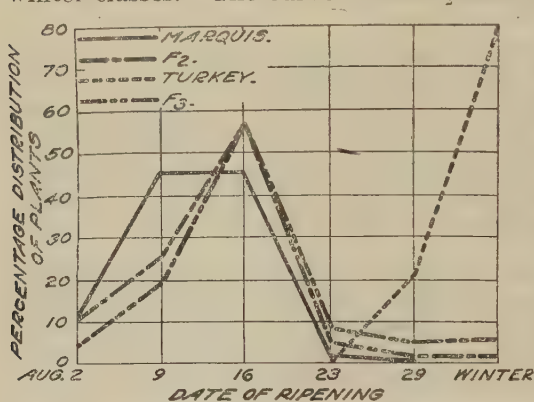


FIG. 3.—Distribution of plants ripening weekly, of Marquis, Turkey, and the F_2 and F_3 generations

late as August 29 were true winter. On this basis, the proportion of spring to winter plants was 35 : 1 for the F_2 , and 7 : 1 for the F_3 . This increase in winter plants in the F_3 generation may be due to either or both of the following reasons: (1) the winter factors, being recessive, breed true, and the percentage of homozygous segregates expected in the F_3 is greater than that expected in the F_2 ; (2) the F_2 , which was the progenitor of the F_3 , was grown from fall sowing and a larger proportion of the true spring segregates may have winter-killed, so these would not appear in the F_3 generation, and the relatively small numbers of F_3 plants ripening August 2 support this supposition.

An early ripening family and a late-ripening family of F_3 were selected as the progenitors of F_4 families. Five F_4 families were grown from the seed of each F_3 family. The seed from the early-ripening F_3 family produced only spring plants. These plants ripened about three days later than Marquis. The seed from the late-ripening F_3 family produced a majority of winter plants. Two

of the five rows produced no spring plants. From these and foregoing data it is evident that the inheritance of winter habit is controlled by multiple factors, and that the date of ripening is influenced by the cumulative effect of these factors.

RELATIONSHIP OF WINTER HABIT AND RESISTANCE

Turkey, as a rule, does not head when spring sown. However, in 1921 about 20 per cent of the plants headed and ripened due to early sowing. These plants were all immune. Evidently the resistance which permitted but 10 per cent of bunt in the fall sowing was able to prevent all bunt from appearing in the spring-sown material. If there is any linkage between winter habit and resistance, the later ripening plants of the F_3 generation should be more resistant than the earlier ones.

The coefficient of correlation between average date ripe and percentage of bunt in the F_3 families was 0.242 ± 0.68 . This shows a slight relationship between early ripening and quantity of bunt produced, but the heterozygous condition of the majority of the families largely masks or lessens the real correlation.

Lateness of ripening due solely to environmental causes might inhibit or retard bunt production. If this were true, the later-maturing plants of Marquis should be freer from bunt than those maturing earliest. This is not the case, but it is rather the reverse, as is shown in Table IX. The F_3 , however, shows a decided tendency toward increased resistance in the later-maturing dates. With the exception of the first ripening date, the F_2 shows greater resistance in the later-ripening plants. The earliest-ripening F_2 plants were very resistant, but the population was small. When the plants ripening on the first two dates are added, the total bunt produced is 8 per cent. This is a third higher than that produced on the later dates.

TABLE IX.—Percentage of bunt produced by Marquis, and the F_2 and F_3 generations of Marquis $\times$ Turkey, on each of the five dates of ripening

Variety	Date	Plants bunt free		Plants all bunt		Plants partly bunt					Total plants (number)	Total bunt (per cent)
		Number	Per cent	Number	Per cent	Number	Per cent	Heads		Per cent bunt		
								Wheat (number)	Bunt (number)			
Marquis	Aug. 2	17	77.3	0	0	5	22.7	51	16	23.9	22	5.4
	Aug. 9	60	67.4	0	0	29	32.6	197	92	31.8	89	10.4
	Aug. 16	60	67.4	0	0	29	32.6	309	110	26.3	89	8.6
	Aug. 23	2	100.0	0	0	0	0	0	0	0	2	0
	Aug. 29	0	0	0	0	0	0	0	0	0	0	0
F ₂	Aug. 2	29	90.6	0	0	3	9.4	32	14	30.4	32	2.9
	Aug. 9	53	67.9	0	0	25	32.1	222	102	31.5	78	10.1
	Aug. 16	151	84.4	2	1.1	26	14.5	291	157	35.0	179	6.2
	Aug. 23	14	87.5	0	0	2	12.5	10	6	37.5	16	4.7
	Aug. 29	4	100.0	0	0	0	0	0	0	0	4	0
F ₃	Aug. 2	181	69.1	4	1.5	77	29.4	645	467	42.0	262	13.8
	Aug. 9	913	72.3	16	1.3	334	26.4	2,665	1,963	42.4	1,263	12.5
	Aug. 16	3,092	82.2	22	.6	649	17.2	6,626	3,010	31.2	3,763	6.0
	Aug. 23	445	89.4	1	.2	52	10.4	457	268	37.0	498	4.0
	Aug. 29	331	90.7	1	.3	33	9.0	237	161	40.5	365	3.8

Since there was no tendency for the later plants of Marquis to be more resistant than the early ones, and this tendency was pronounced in both the F_2 and F_3 generations, it is evident that either there is some linkage between winter habit and bunt resistance, or that the cumulative effect of the factors for winter habit which cause difference in date of ripening also have an inhibiting effect upon bunt production.

Twenty-two of the 44 immune F_3 families produced no winter plants, and 17 ripened at least two weeks earlier than Turkey. If winter habit were completely linked with the AA resistance, all the immune segregates should resemble Turkey in date of ripening as well as in bunt resistance. This is impossible, however, if the assumption is correct that Turkey resistance is caused by a single factor and winter habit is caused by multiple factors. The winter-habit factors segregate as shown by the occurrence of spring types that mature later than Marquis. Linkage between resistance and one of the winter-habit factors would account for the increased resistance of the later maturing F_3 plants. The simplest interpretation, however, seems to be that there is little or no linkage between winter habit and bunt resistance, but that the factors for winter habit also cause increased resistance to a limited extent by means of some inhibiting influence.

AWNLESSNESS

The F_1 plants of Marquis $\times$ Turkey were all intermediate for awnlessness, having short awns on the upper florets of the head. The F_2 rows produced both awnless and awned plants. The number and per cent of plants in each class for each family is shown in Table X.

TABLE X.—Number and percentage of awnless and awned plants in five F_2 families of Marquis $\times$ Turkey

Row No.	Number of plants			Per cent population	
	Awnless	Awned	Total	Awnless	Awned
402901.....	162	47	209	77.5	22.5
403001.....	144	60	204	70.6	29.4
403101.....	95	66	161	59.0	41.0
403201.....	127	38	165	77.0	23.0
403301.....	175	72	247	70.9	29.1
Total.....	703	283	986	71.3	28.7

In making the separation in Table X, only the fully awned plants were considered awned. Those which were entirely awnless or which were somewhat intermediate were recorded as awnless. The number of plants in each family is fairly large, and the variation from the expected 3 : 1 ratio is rather wide.

The F_2 row (403201), which most nearly approached the 3 : 1 ratio, was selected as the progenitor of the F_3 generation. On account of the small number of seeds produced by some of the awned plants, the seed from five of these was not sown. The 33 awned F_2 plants which were saved produced only awned segregates in the F_3 . The

awnless F_2 plants produced 35 homozygous awnless families, and 92 heterozygous ones. The genetic segregation of the F_2 family, as shown by the performance of the F_3 , was 35 awnless : 92 heterozygous : 33(+5) awned. The expected monohybrid ratio of the same population is 41 : 83 : 41. The fact that the awned recessives all bred true makes the unit-factor hypothesis the most plausible. This explanation is in accord with results of other crosses in which Turkey was used as the awned parent (Table II), and is in harmony with Percival's interpretation (13).

LINKAGE OF AWNS AND RESISTANCE

There were four F_3 families which had fewer than 10 plants in either the fall or spring sowing, and since these were not considered in studying the inheritance of resistance they are disregarded. The number of awnless, heterozygous, and awned families, and the average per cent of bunt produced in each sowing, are shown in Table XI.

TABLE XI.—Number of awnless, heterozygous, and awned F_3 families of Marquis $\times$ Turkey and percentage of bunt produced by each genotype in fall and spring sowings

Genotype	Number of rows	Per cent bunt from	
		Fall sown	Spring sown
Awnless.....	34	67.8	10.0
Heterozygous.....	90	49.4	6.2
Awned.....	32	54.2	4.5

If only the awnless and awned genotypes are considered, it appears that there is some linkage between awns and the a factor for bunt resistance. However, the F_2 plants heterozygous for awns when fall sown produced less bunt than the awned, which is not to be expected if there is linkage. The heterozygous spring-sown families produced an intermediate amount of bunt which would be expected in case of linkage. The fact that 8 of the 44 immune families were awnless, 9 awned, and 27 heterozygous, indicates that there was little if any linkage between awns and the a factor for resistance.

LINKAGE OF AWNS AND WINTER HABIT

Seventy-one of the F_3 families produced one or more plants of winter habit of growth. Awnless, mixed, and awned families occurred in almost exactly the same proportion as in the pure spring group (14 : 41 : 16 compared with 21 : 51 : 17). If the awned character were connected in any way with winter habit, the group with winter plants should have a larger proportion of awned families, because Turkey carried both awns and winter habit. The foregoing ratio does show a slight tendency toward an increase in awning such as might be expected if the gene for awns were carried in one of three chromosomes carrying factors which delay the ripening period. If such were the case and there were no crossing over, it would be impossible for an awned family to ripen as early as Marquis. This is what actually happened, as shown in Table XII.

TABLE XII.—Number of awnless, heterozygous, and awned F_3 families throwing winter plants; also average date ripe of each genotype

Genotype	Number of families			Mean date ripe		
	True spring	Not true spring	Total	Earliest family	Latest family	Average all families
Awnless.....	21	14	35	Aug. 8	Aug. 27	Aug. 16
Heterozygous.....	51	41	92	...do....	Aug. 29	Do.
Awned.....	17	16	33	Aug. 13	Aug. 28	Aug. 17

The earliest awned row ripened five days later than the earliest awnless row. This might be mere coincidence, as the average of all awned families is but one day later than that of the awnless rows. The number of families is scarcely adequate for determining ratios where three factors are involved.

SUMMARY AND CONCLUSIONS

Marquis, when spring sown, is highly resistant to bunt; but when fall sown, it is comparatively susceptible. However, the resistance is not entirely inhibited by the winter resting period.

Turkey, when fall sown, is highly resistant; and when spring sown, is immune.

Transgressive inheritance occurred in both the fall and spring sowings of the F_3 Marquis $\times$ Turkey. Evidently the resistance of the parents is caused by different factors.

A correlation coefficient of 0.711 ± 0.027 was obtained between the amount of bunt produced by the fall-sown and the spring-sown F_3 families. This indicates that the factors which cause resistance in the fall sowing are also operative in the spring sowing.

Resistance in the cross between Marquis and Turkey is apparently caused by two factors, the one carried by Turkey being much more "prepotent" than the one carried by Marquis.

The ratio of spring to winter plants was 35 : 1 in the F_2 population, and 7 : 1 in the F_3 . This not only indicates that partial dominance of spring habit, but also that the inheritance of winter habit is controlled by multiple factors.

The later-ripening spring plants of the F_2 and F_3 generations were more resistant than the early ones.

Although the ratio of awnless to awned plants in the F_2 was only 2.5 : 1, all awned plants bred true in the F_3 , indicating that awns are inherited as a unit character.

The awned F_3 families were somewhat more resistant than the awnless ones. However, the fact that only 9 of the 44 immune spring families were awned while 8 of them were awnless, indicates that there is little if any linkage between awns and resistance.

The average date ripe of the awnless, intermediate, and awned F_3 families was approximately the same. The ratio of awnless to awned families in the group which produced one or more winter plants and in the true spring group was approximately the same. If there is any linkage between awns and winter habit, the number of families is too small to determine it.

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